



Home range size and spatial organization of Swift fox *Vulpes velox* (Say, 1823) in southeastern Wyoming

By P. PECHACEK, F. G. LINDZEY, and S. H. ANDERSON

Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, USA

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Abstract

We investigated home-range size and spatial arrangement of swift fox *Vulpes velox* (Say, 1823) between September 1996 and March 1997 in a sagebrush-grassland habitat in southeastern Wyoming. Home-ranges ($\bar{x} \pm \text{SE}$, $n = 10$) averaged 11.7 ± 1.3 and $7.7 \pm 1.1 \text{ km}^2$ using the 95% adaptive kernel method and the 100% minimum convex polygon, respectively. Although the ranges of males seemed about 25% larger compared with females, the difference was not significant. Core areas (50% utilization distribution) consisted of 1 or 2 polygons and averaged $19.0 \pm 2.6\%$ of the total home-range area. Home-range overlap of paired foxes (95% adaptive kernel: $59.6 \pm 7.9\%$; $n = 8$ combinations) was significantly greater than range overlap of unpaired animals (95% adaptive kernel: $9.9 \pm 2.8\%$; $n = 18$ combinations). Paired foxes shared more than 70% of their dens. 75% of the dens were located within an individual's core area. Our results suggested that swift foxes were monogamous.

Key words: *Vulpes velox*, home-range, spatial organization

Introduction

Foxes, which include the smallest canids, are extremely variable in their social structure, which ranges from solitary through monogamous to cooperative (SANDELL 1989). However, most of the fox species investigated to date generally fit the pattern predicted by MOEHLMAN (1986, 1989), and confirmed by HERSTEINSSON and MACDONALD (1982): they are usually monogamous, but tend toward polygyny more than larger canids.

The recently declining swift fox *Vulpes velox* (Say, 1823) inhabiting the prairies of the Great Plains belongs to the smallest North American canids. Nocturnal swift foxes appear to be monogamous (SETON 1927), but some polygamy may take place (KILGORE 1969). However, data supporting this are lacking (EGOSCUE 1979; SCOTT-BROWN et al. 1987). Polygamous units throughout the year have been often reported in the closely related and more investigated kit fox *Vulpes macrotis* (MERRIAM, 1888) (EGOSCUE 1956, 1962, 1975; MORRELL 1972). Thus, similar findings for the swift fox could be expected.

Because the social structure is largely reflected by the spatial relationships between neighboring foxes, exploration of home-range overlap along with home-range size in different sexes may help to evaluate the social system in free-ranging foxes (GEFFEN and MACDONALD 1992; ZOELICK and SMITH 1992). Therefore, we focused our efforts on studying the swift fox's space use patterns. Our objective was to determine the size and spatial organization of home-ranges in the sagebrush-grassland habitat of southeastern Wyoming during the dispersal, breeding, and gestation period of the swift fox.

Material and methods

The 280-km² study area near Medicine Bow, Wyoming, (42°N, 106°W) is primarily used for cattle grazing. The site is a sagebrush-grassland community 2,070 m above sea level with low annual precipitation (< 300 mm). The topography is flat to mildly undulating with numerous dry lakebeds. With some exceptions (fencelines, secondary dirt roads etc.), there is little human development in the area.

Foxes were captured in March 1996, radio-collared with 45-g transmitters (Advanced Telemetry Systems, Isanti, Minnesota, USA) and released. Our trapping effort was designed to trap all the foxes living in the study area, and thus traps were equally spread all over the place. All captured animals were > 1 year of age. Between September 1996 and March 1997, 10 swift foxes were relocated on a weekly basis. Owing to the swift fox's nocturnal activity patterns, we attempted to obtain one location for each collared fox for each night we were in the field for that week. Dens were located during the day between successive nights. We used a Telonics TR-2 Receiver (Telonics, Mesa, Arizona, USA) and a combination of truck roof-mounted dipole antenna and a hand-held, two-element H-antenna to estimate locations using triangulation.

Consecutive observations of the same fox were separated by > 12 hs to avoid autocorrelation (SWIHART and SLADE 1985; WHITE and GARROTT 1990). Radio-locations including 95% error ellipses were calculated using the maximum likelihood technique (LENTH 1981) in program LOCATE II, version 1.3 (Pacer, Truro, Nova Scotia, Canada). The observer's position was determined by a Global Positioning System (GPS) Magellan 1000 (Magellan Systems Corporation, San Dimas, California, USA). To provide a reasonable home-range estimate, we excluded locations with > 3.0 km² error ellipse from the analysis. We also excluded inactive locations (i.e. resting in a den) to avoid undue influence on measures of range utilization (WHITE et al. 1996). The 95% error ellipse of selected radio-locations averaged 0.39 ± 0.05 km² ($n = 203$). We finally analyzed range use of 6 males and 4 females (including 4 pairs) using 225 locations (22.5 ± 2.3 , range 19–26 locations/fox).

We computed the median center of activity (MOHR and STUMPF 1966) for each fox. Home-ranges were estimated using the adaptive kernel model (WORTON 1989) in the program CALHOME (KIE et al. 1996). We calculated the 50% and 95% utilization distribution (UD) as point percentage contours using least-squares cross-validation to choose the optimum kernel bandwidth (smoothing parameter). Den locations were plotted on a map to examine their distribution with distributions of core areas (50% UD). We also calculated home-ranges using the 100% minimum convex polygon, MCP (MOHR 1947), to obtain comparability with data which were already published. Home-range size between sexes was compared by the independent t-test using the pooled variance estimate method (BROSIOUS 1988).

The number of locations needed to obtain asymptotic home-range estimates (area-observation curve) was evaluated for each individual fox (GAUTESTAD and MYSTERUD 1995). To determine this, we plotted home range size vs. decreasing number of locations removing 2 and 4 randomly chosen observations from the total number of locations, and then we evaluated the magnitude of changes in such an altered home-range size (HARRIS et al. 1990).

Foxes were considered paired (mates) if they frequently and concurrently shared a den (EGOSCUE 1975). Locations from mates were pooled to calculate the total home-range of fox pairs. We classified foxes with adjacent home-ranges (neighbors) as paired male-female combination (paired M-F) or unpaired male-female (unpaired M-F), female-female (F-F), or male-male (M-M) combination.

Overlap of home-ranges and core areas between foxes was evaluated with the Mann-Whitney U-test for unpaired combinations (independent samples) and by the Wilcoxon test for paired foxes (related samples). We examined whether use within overlapping areas differed from use within non-overlapping proportions of home-ranges by comparing the frequency of locations in the overlap areas with an expected frequency (Chi²-test). The expected frequency was based on the proportion of the home-range in the overlap area.

Standard deviations were given with means ($\bar{x} \pm SD$) unless stated otherwise. Statistical significance was set at $P < 0.05$.

Results

Number of locations/fox needed to obtain asymptotic home range estimates averaged 16.0 and 17.1 for the adaptive kernel ($n = 8$) and MCP model ($n = 10$) respectively (range 11 to 20). Using the 95% adaptive kernel model, home ranges reached on average $98.8 \pm 13.8\%$ and $103.7 \pm 17.4\%$ of their original size with the subtraction of the $n - 4$

Table 1. Estimates of home-range size (km²) using minimum convex polygon (100% MCP; MOHR 1947) and adaptive kernel estimator (95% with 50%; WORTON 1989) for swift fox at Medicine Bow, Wyoming, 1996–1997.

	n	MCP				adaptive kernel				
		\bar{x}	SD	range	\bar{x}	SD	range	\bar{x}	SD	range
F	4	6.3	2.2	3.5– 8.7	9.8	2.6	6.5–12.0	1.6	0.8	1.0–2.7
M	6	8.7	4.0	5.5–15.9	13.0	4.7	7.9–19.4	2.6	0.9	1.8–4.0
All	10	7.7	3.5	3.5–15.9	11.7	4.1	6.5–19.4	2.2	1.0	1.0–4.0

and $n - 2$ random radio-locations, respectively (where n equals the total number of locations a fox was sampled). The MCP produced even a smoother asymptote: $92.4 \pm 6.0\%$ ($n - 4$) and $97.4 \pm 5.0\%$ ($n - 2$).

Home-ranges of males were larger compared to the females (Tab. 1), but the difference was not significant (95% UD: t-test; $t = -1.2$, 8 df, $P = 0.257$; 50% UD: t-test, $t = -1.9$, 8 df, $P = 0.107$). Core areas contained $19.0 \pm 8.3\%$ of total home-range area. We identified an average of 1.5 ± 0.5 core area polygons per home-range with no differences between sexes (t-test, $t = 1.3$, 8 df, $P = -0.242$). Total area of home-ranges of 4 fox pairs averaged 15.98 ± 2.49 km² (95%, adaptive kernel) and 13.72 ± 4.64 km² (MCP).

Nearly all home-ranges bordered or overlapped those of their neighbors (Fig. 1). Home-ranges of mates ($n = 8$) overlapped an average of $59.6 \pm 22.4\%$ (95% adaptive kernel) whereas core areas overlapped by $37.9 \pm 20.7\%$. In both, we did not detect a difference if measuring ranges of females overlapped by males or vice versa (Wilcoxon test), a) home-range: $Z = -1.1$, $P = 0.273$, b) core area: $Z = -1.5$, $P = 0.144$). Home-ranges of 4 adjacent females overlapped $5.3 \pm 1.4\%$. Home-ranges of 6 adjacent males overlapped on average $9.6 \pm 15.0\%$, but 4 males had no home-range overlap at all. Thus, overlap between F-F and M-M combination did not differ significantly (Mann-Whitney U-test: $Z = -0.9$, $P = 0.379$). Shared area of 8 adjacent, unpaired M-F combinations averaged $12.5 \pm 13.0\%$ with no difference between sexes (Mann-Whitney U-test: $Z = -0.1$, $P = 0.885$). In summary, home-range overlap combined for all possible combinations of adjacent foxes averaged $9.9 \pm 12.0\%$ between those classified as unpaired (4 F-F + 6 M-M + 8 M-F; $n = 18$). This was significantly less than the overlap between mates (Mann-Whitney U-test: $Z = -4.0$, $P = 0.0001$). Core areas of unpaired foxes did not overlap.

We measured utilization intensity in shared areas comparing the observed number of locations with the expected number of locations. In 14 of 20 comparisons, the number of locations within areas of range overlap did not differ from expected. However, in 3 of 7 comparisons, females overlapping the ranges of other females or males overlapping females other than their mates, used the shared areas less than expected. Conversely, we located a fox in the area shared with its mate more than expected (males: 2 of 4 comparisons; females: 1 of 3 comparisons). We examined overlapping core area use between paired foxes in 8 cases. Seven of the 8 cases indicated use was as expected. In 1 case a use by a male was less than expected.

Nine foxes were located in as many as 6 different dens. We found that $75.1 \pm 27.2\%$ ($n = 24$) of dens belonging to an individual fox were located within its core area. The distance between the median center of activity of 9 individual foxes and their den sites averaged 824 ± 491 m ($n = 34$). Paired foxes ($n = 3$) shared most dens (males: $70.3 \pm 26.3\%$, females: $81.9 \pm 18.8\%$). Total common core areas of the 4 fox pairs contained $84.6 \pm 10.8\%$ of their shared dens. Female swift foxes were located in approximately 60% of cases in a den with their mate (range 42–85%; $n = 3$).

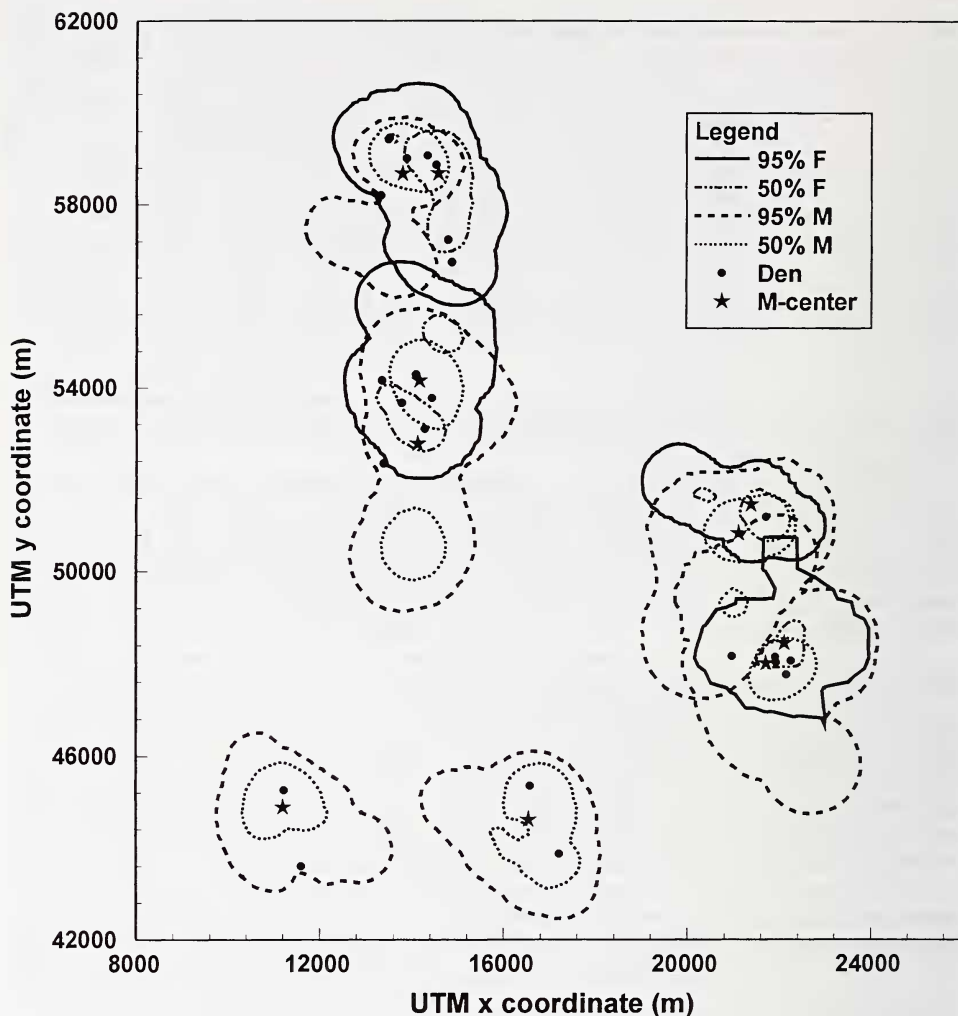


Fig. 1. The spatial organization of home-ranges [95% utilization distribution (UD)] and core areas (50% UD) of 10 radio-collared swift foxes at Medicine Bow, Wyoming, 1996–1997. Home-ranges were plotted using the adaptive kernel method. Note also the distribution of median center of activity and den sites.

Discussion

Size of home-range scales with body size in carnivores (GITTLEMAN and HARVEY 1982; LINDSTEDT et al. 1986). Although male swift foxes are slightly heavier than females (KILGORE 1969), we found no effect of sexes on sizes of home-ranges or core areas. Home-ranges during the dispersal, breeding, and gestation period (September–March) in our study area were considerably smaller than estimates of home-range sizes (11.2–32.3 km²) elsewhere in swift fox's geographic range (SHARPS and WHITCHER 1984; HINES and CASE 1991). Related kit foxes were reported having home-ranges from 1.4–11.6 km² (MORRELL 1972; DANEKE et al. 1984; O'NEAL et al. 1987; ZOELLICK and SMITH 1992; WHITE and

RALLS 1993; CORREA 1996). Small ranges of the swift fox we documented in Wyoming may not have been influenced by the relatively low number of individual's relocations, since we proved based on the area-observation curve that the given number of relocations (19–26 per fox) adequately estimated the home-range size. However, the home-ranges may have been larger had we included the summer months.

Given the parental investment hypothesis stated by MOEHLMAN (1986), small North American foxes should more likely be polygynous than larger canids. Thus, appreciable home-range overlap among adjacent foxes may be predicted. Overlapping swift fox ranges were not measured, yet. However, the kit fox has been observed having overlapping home-ranges between 56–83% in paired individuals, and up to 25% in non-paired individuals (DANEKE et al. 1984; ZOELICK and SMITH 1992; WHITE and RALLS 1993; CORREA 1996). Core areas (50% harmonic mean isopleths) were used by kit foxes exclusively (WHITE and RALLS 1993) or overlapped by 59% only between family members (CORREA 1996).

Overlap of home-ranges in our study was extensive between individuals classified as mated pairs, but was low outside of this category, a relationship contrary to the hypothesized polygyny. Because the home-range of a given male overlapped extensively with only one female, opportunities for multiple matings by males may have been limited. Consequently, nocturnal activity centers of paired individuals were close together and mates tend to use overlap area slightly more than expected by its proportion. We found some overlap of home-ranges between unpaired individuals, but those foxes seemed to visit their overlap areas less than expected. Moreover, the lack of core area overlap between unpaired foxes may indicate that a portion of the home-range at den sites was used exclusively. Our sample of 10 foxes was clearly limited to allow overall conclusions, but the results were consistent with a social organization in which mated pairs occupy areas that overlap little with those of adjacent pairs.

Extensive overlap of home-range between pair members, no intersexual difference in size of home-range, and slight physical dimorphism were defined by GEFFEN and MACDONALD (1992) as indicators of monogamy in canids. Hence, our results suggested that swift foxes were monogamous without tending toward polygyny as expected relating to body mass and behavioral trends in canids (MOEHLMAN 1986, 1989). However, some evidence for polygamous units in swift fox has been supported by the fact, that overlap of unpaired M-F combinations was greater than overlap of F-F, and M-M combinations possibly indicating mutual attraction of unpaired foxes.

Spatial organization between neighboring foxes can only be a meaningful reflection of the social system, if all animals in the neighborhood have been tracked. However, little overlap between unpaired foxes in this study may also be influenced by some undetected foxes which may not have been captured. Even if the spatial relationships between neighboring foxes largely reflected their social structure, exploration of home-range overlap and home-range size were not sufficient criteria to confirm their mating system per se. Evaluation of social structure in the swift fox had have required direct observations of social interactions to rule out all social arrangements. Social organization of carnivores can vary with another ecological factors such as availability and dispersion of resources, habitat type and quality, population density, and season (MACDONALD 1983). Despite of some potentially valuable information about space use by swift foxes, the results of our study are of limited scope to provide inference to larger populations.

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Zusammenfassung

Aktionsraumgröße und Raumorganisation beim Swiftfuchs (Vulpes velox Say, 1823) im südöstlichen Wyoming

Die Aktionsraumgröße und Raumorganisation beim Swiftfuchs wurden zwischen September 1996 und März 1997 untersucht, um mit Hilfe von Radiotelemetrie die soziale Struktur in einer kleinen Population in der Prärie des südöstlichen Wyoming zu beschreiben. Die durchschnittliche Aktionsraumgröße anhand der 95% adaptiven Kernel Methode betrug $11.7 \pm 1.3 \text{ km}^2$ ($x \pm \text{SE}$, $n = 10$). Streifgebiete der Männchen waren um ca. 25% grösser als die der Weibchen, allerdings war dieser Unterschied nicht signifikant. Gebiete mit der Nutzungsverteilung von 50% (Kerngebiet) hatten an der Gesamtgröße des Aktionsraums einen Anteil von $19.0 \pm 2.6\%$ und setzten sich aus 1 oder 2 Polygonen zusammen. Die Überlappung der Streifgebiete war bei den verpaarten Individuen mit $59.6 \pm 7.9\%$ ($n = 8$ Kombinationen) signifikant größer als die Überlappung der Aktionsräume unverpaarter Füchse ($9.9 \pm 2.8\%$; $n = 18$ Kombinationen). Verpaarte Füchse teilten sich mehr als 70% ihrer Baue, wobei sich 75% der Baue im Kerngebiet der jeweiligen Tiere befand. Die beobachteten Füchse verhielten sich monogam.

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Authors' addresses: PETER PECHACEK, Nationalparkverwaltung Berchtesgaden, Doktorberg 6, D-83471 Berchtesgaden, Germany (e-mail: pechacek@forst.uni-muenchen.de); FREDERICK G. LINDZEY and STANLEY H. ANDERSON, Wyoming Cooperative Fish and Wildlife Research Unit, Box 3166, University Station, Laramie, WY 82071, USA